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PHOTOSYNTHETIC RESPONSES TO IRRADIANCE IN THREE FOREST UNDERSTORY SPECIES OF THE C_4 GRASS GENUS MUHLENBERGIA[1]

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Three species of the C_4 grass genus *Muhlenbergia*—*M. frondosa, M. sobolifera,* and *M. schreberi*—were collected from forest understory habitats in Kansas and grown in a growth chamber at 1,500, 150, and 15–25 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD). Assimilation (A), conductance to CO_2, intercellular CO_2 concentration, chlorophyll (chl) concentrations, and photosystem I electron-transport capacity were determined and compared with results for *M. cuspidata,* which occurs only in open, prairie areas. All of the shade species exhibited more shade tolerance than the prairie species: they had lower maximum A, saturation of A, and photosystem I electron transport with respect to PPFD, higher quantum yields that increased with decreasing growth PPFD, and increasing chl concentrations with decreasing PPFD.

Introduction

Plants from shaded habitats generally have lower photosynthetic rates than sun plants at saturating PPFD, but relatively high rates at low PPFD (BJÖRKMAN and HOLMGREN 1963). When grown at a range of PPFD, sun and shade plants respond differently, indicating adaptation to a particular PPFD (BJÖRKMAN and HOLMGREN 1963; BJÖRKMAN et al. 1972; AGATA et al. 1985).

Shade plants often have greater chl concentrations on a weight basis and lower chl a/b ratios than sun plants (BOARDMAN 1977; BJÖRKMAN 1981). Both characteristics are thought to enhance light capture in environments with low PPFD. Therefore, an examination of chl concentrations may reveal a physiological adaptation to a particular level of PPFD.

Higher rates of A at light saturation in sun plants may be a consequence of changes in internal leaf morphology (NOBEL 1976; NOBEL and LONGSTRETH 1981; LONGSTRETH et al. 1985). In some species, a strong positive correlation between photosynthetic rate on a leaf surface area basis and A_{mes}/A (mesophyll cell surface area to leaf surface area) has been demonstrated (NOBEL et al. 1975; ÖQUIST et al. 1982). Other species have not always shown such a strong correlation between the two factors (CHABOT and CHABOT 1977; LONGSTRETH et al. 1981).

Another indicator of adaptation to light in plants is the rate of photosynthetic electron transport. Increased PPFD during growth substantially increases the capacity for light-saturated electron transport in many species (BJÖRKMAN et al. 1972; ÖQUIST and HELLGREN 1976). Furthermore, shade plants have lower electron-transport capacities than sun plants (BJÖRKMAN et al. 1972; BOARDMAN 1972).

C_4 plants have a higher ATP requirement than C_3 plants and exhibit characteristics typical of sun plants (PEARCY and EHLERINGER 1984). However, recent work with C_4 plants collected from forest understories indicates that the C_4 syndrome may not impose an inherent limitation on the ability of a plant to adjust to a wide range of light levels (BROWN 1977; PEARCY et al. 1982; WINTER et al. 1982; WARD and WOOLHOUSE 1986).

To provide a better understanding of the potential for shade tolerance in C_4 plants, the photosynthetic responses of three species of the C_4 grass genus *Muhlenbergia* collected from understory habitats—*M. frondosa, M. sobolifera,* and *M. schreberi*—were compared with those of a related species, *M. cuspidata,* which is confined to exposed environments. Photosynthesis, chl concentrations, and photosystem I electron-transport capacity were measured as indicators of the degree of photosynthetic adaptability to PPFD.

Material and methods

Muhlenbergia frondosa (Poir.) Fern., *M. sobolifera* (Muhl.) Trin., and *M. schreberi* Gmel. were collected from a forest understory and *M. cuspidata* (Torre.) Rydb. from an open prairie. Collection sites and details of growth conditions are described by SMITH and MARTIN (1987).

The collected plants were potted and grown in a growth chamber under three light regimes: 1,500, 150, and 15–25 μmol m^{-2} s^{-1} for 30–40 days for gas-exchange measurements, 28 days for pigment analyses, and 28–35 days for photosystem I measurements. Plants were maintained under a 12-h photoperiod, 30/25 C day/night, and 15%/25% day/night RH.

[1]Abbreviations: A, assimilation; A_{mes}/A, area of the mesophyll/leaf area; chl, chlorophyll; c_i, intercellular CO_2 concentration; g_c, conductance to CO_2; LSD, least significant difference; MV, methyl viologen; PPFD, photosynthetic photon flux density.

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Photosynthetic gas exchange

Photosynthetic responses to instantaneous PPFD were determined for all species with a gas-exchange system identical with that described in Martin and Zee (1983), except that a water-jacketed polycarbonate chamber with an 8.75-cm^3 volume was used. The flow rate through the chamber was ca. 1.5 L min^{-1}, and the turnover time for chamber air was ca. 0.35 s. Maximum air turbulence in the chamber was maintained by varying the angles and positions of the 10 air-inlet and -outlet holes. Light was provided by a 400-W multivapor metal halide lamp with a spectral irradiance peak at 600 nm and was decreased with layers of cheesecloth (Brown 1968). PPFD levels were determined at the chamber surface (transmittance ca. 90%) with a LI-COR (Lincoln, Neb.) LI-190SB quantum sensor and LI-185B meter.

Gas-exchange measurements were taken at 11 PPFD levels after allowing the system to achieve a steady-state rate of gas exchange at each PPFD level: 0, 10, 20, 25, 65, 105, 150, 250, 300, 700, and 1,500 μmol m^{-2} s^{-1}. This usually occurred within 10–45 min. If the rate did not reach steady state within 45 min, the PPFD level was increased. Experiments were initiated in darkness, and PPFD was increased incrementally to 1,500 μmol m^{-2} s^{-1} and then lowered to several intermediate levels to check for irreversible damage to the leaves. Such damage was never observed. Leaf temperature was maintained at 30 C; air temperature varied from 26 to 30 C, and vapor pressure deficit from 1.75 to 2.80 kPa (Martin and Zee 1983). Mean CO_2 concentration was 354 μL L^{-1} (SD = 10, no. = 108).

Gas exchange was measured on three attached leaves per plant from three plants for each species at each growth PPFD. The portions of the attached plants outside the chamber were covered with cheesecloth, and the plants were watered as needed during measurements to protect them against heat and desiccation damage.

On completion of the gas-exchange measurements, the leaves were removed from the chamber to measure leaf area with a LI-COR LI-3000 leaf area meter. Chl concentrations were determined. CO_2- and H_2O-exchange data were calculated (Šesták et al. 1971); and A, g_c, and c_i were calculated using equations from Farquhar and Von Caemmerer (1982). Quantum yields for CO_2 uptake were calculated as the slope of the linear relationship between incident PPFD (0–150 μmol m^{-2} s^{-1}) and CO_2 exchange.

All gas-exchange data were analyzed using a two-way ANOVA (SPSS^x, Chicago, Ill.), and mean values for A, g_c, and c_i at maximum instantaneous PPFD were compared for LSD (Sokal and Rohlf 1981). Statistical difference was inferred when $P < .05$.

A_{mes}/A determinations

Fresh leaf sections were prepared to determine A_{mes}/A ratios (Smith and Martin 1987). Measurements of A_{mes}/A ratios for *M. frondosa, M. sobolifera,* and *M. schreberi* were made, assuming the cells to be spherical (Nobel et al. 1975). For *M. cuspidata,* which has radiating cylindrical mesophyll surrounding each bundle sheath, cells were assumed to be cylinders with hemispherical ends (Nobel et al. 1975). Ratios were calculated, including interstitial mesophyll cells on either side of the bundle sheaths. A_{mes}/A ratios were analyzed using the Kruskal-Wallace test for nonparametric data, and means were compared using the Mann-Whitney *U*-test (Sokal and Rohlf 1981). Statistical difference was inferred when $P < .05$.

Pigment analyses

The first mature leaf from three to 10 plants of each species at each light level was clipped; its area was measured; and chl determinations made (Martin et al. 1985). All pigment data were statistically analyzed by ANOVA, and means were compared for LSD (Sokal and Rohlf 1981). Statistical difference was inferred when $P < .05$.

Photosynthetic electron-transport capacity

Preparation of chloroplasts for measurement of photosystem I activity followed Robinson and Yocum (1980). Leaves (1–5 g) were removed from mature plants, cut into small pieces, and ground at 5 C with a mortar and pestle in a minimal amount of extraction buffer (pH 7.5), consisting of 0.4 M sucrose, 20 mM HEPES, 5 mM $MgCl_2$, 0.15 M NaCl, and 0.2% BSA (Robinson and Yocum 1980). The slurry was ground until examination under a light microscope revealed that the bundle sheaths were obliterated, filtered through four layers of cheesecloth, and centrifuged at 200 *g* for 2 min at 5 C. The pellet was discarded; the supernatant was spun at 1,475 *g* for 10 min, recovered, and centrifuged again at 1,475 *g* for an additional 10 min. The supernatant was then frozen at −80 C and stored until needed (1–6 wk), whereupon it was thawed on ice and chl concentration was determined. No effects of cold storage were evident; full-scale absorption spectra revealed no peaks attributable to pheophytin.

The photoreduction of MV as an indicator of photosystem I electron-transport capacity was determined (Katoh 1972) by following the absorption of oxygen in a reaction mixture (pH 7.8) containing 20 mM Tris HCl, 0.1 mM MV, 0.04 mM 2,6 dichlorophenolindophenol (DCIP), 2mM ascorbate, 10 μM (3-[3,4-dichlorophenyl])-1, 1-dimethylurea (DCMU), and 1 mM sodium azide. Nine mL of the above reaction mixture, 80 μg chl, and sufficient distilled water to complete the volume

were placed in an 18-mL glass water-jacketed chamber and stirred continuously with a magnetic stir bar. Oxygen absorption was measured with a YSI (Yellow Springs, Oh.) R-5521-00 oxygen electrode and R-5514 meter at nine PPFD levels (0, 5, 10, 25, 40, 80, 150, 500, and 1,500 μmol m^{-2} s^{-1}). Light (Bausch and Lomb optical unit with a 500-W lamp) was measured at the outer surface of the chamber. The light beam passed through a heat filter of 30 cm water that maintained the reaction mixture at 21–23 C during measurements. Three plants of each species at each growth PPFD were analyzed; the chamber was flushed with deionized water between experiments. All data were statistically analyzed in the same manner as in the gas-exchange measurements.

Results

Photosynthetic gas exchange

Growth PPFD had a significant effect on photosynthetic responses to PPFD in *Muhlenbergia frondosa* (fig. 1*A*), *M. schreberi* (fig. 3*A*), and *M. cuspidata* (fig. 4*A*), but not in *M. sobolifera* (fig. 2*A*). Light saturation of photosynthesis occurred at ca. 250–400 μmol m^{-2} s^{-1} for *M. frondosa*, *M. sobolifera*, and *M. schreberi* grown at all PPFD levels and for *M. cuspidata* grown at medium and low PPFD. *Muhlenbergia cuspidata* grown at high PPFD failed to show photosynthetic saturation with respect to PPFD.

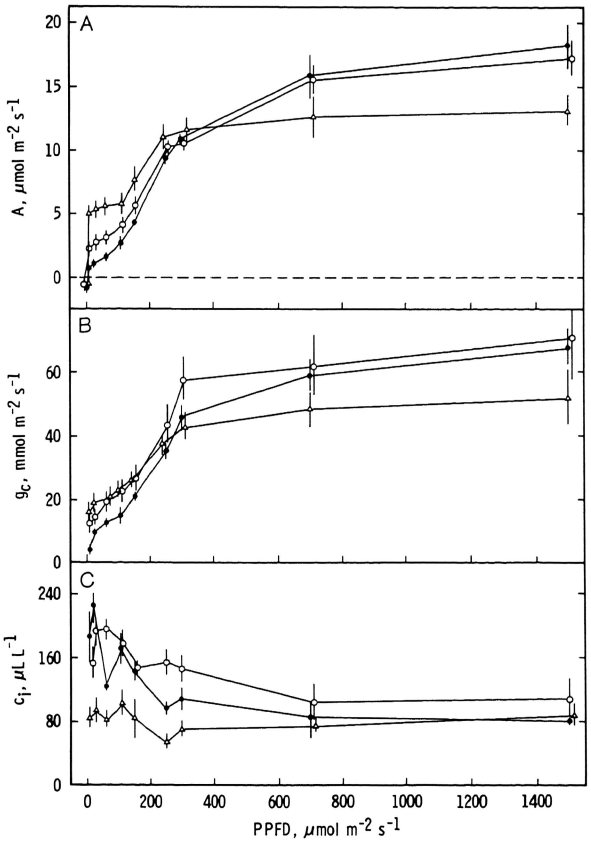

FIG. 1.—*A*, Assimilation rate (A); *B*, leaf conductance (g_c); and *C*, intercellular CO_2 concentration (c_i) as functions of PPFD in *Muhlenbergia frondosa*. Plants were grown for 30–40 days at the following PPFD levels: ●, High = 1,500 μmol m^{-2} s^{-1}. ○, Medium = 150 μmol m^{-2} s^{-1}. △, Low = 15–25 μmol m^{-2} s^{-1}. Data are means and SE of three plants.

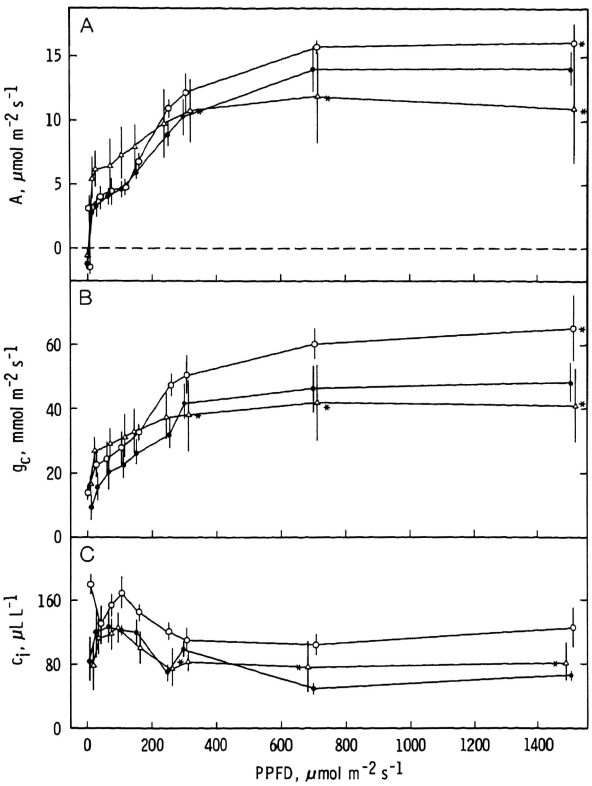

FIG. 2.—*A*, Assimilation rate (A); *B*, leaf conductance (g_c); and *C*, intercellular CO_2 concentration (c_i) as functions of PPFD in *Muhlenbergia sobolifera*. Plants were grown for 30–40 days at the following PPFD levels: ●, High = 1,500 μmol m^{-2} s^{-1}. ○, Medium = 150 μmol m^{-2} s^{-1}. △, Low = 15–25 μmol m^{-2} s^{-1}. Data are means and SE of three plants. Asterisks indicate non-steady-state results.

Maximum A in *M. frondosa* was higher at high instantaneous PPFD in plants grown at high and medium PPFD than at low PPFD (fig. 1*A*). *Muhlenbergia schreberi* grown at medium PPFD exhibited higher maximum A (fig. 3*A*) compared to plants grown at high and low PPFD, whereas plants of *M. cuspidata* grown at high PPFD exhibited higher rates than at medium and low PPFD (fig. 4*A*).

In plants from all growth regimes, g_c generally increased in conjunction with A in response to increasing instantaneous PPFD in all four species (figs. 1*B*, 2*B*, 3*B*, 4*B*). *Muhlenbergia frondosa* (fig. 1*B*) and *M. schreberi* (fig. 3*B*) grown at high and medium PPFD had equally high maximum g_c. However, g_c was highest in plants grown at medium

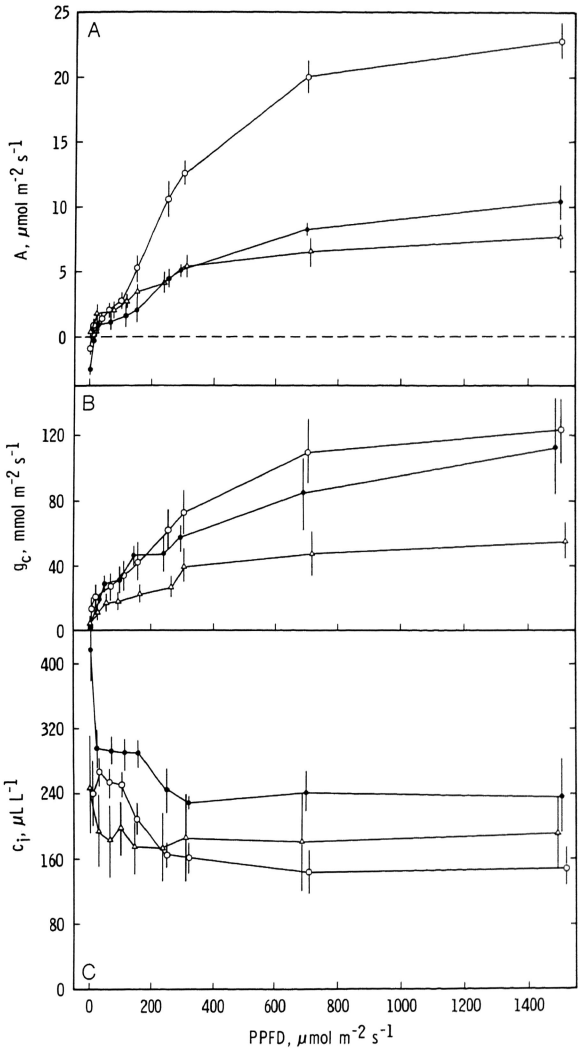

FIG. 3.—*A*, Assimilation rate (A); *B*, leaf conductance (g_c); and *C*, intercellular CO_2 concentration (c_i) as functions of PPFD in *Muhlenbergia schreberi*. Plants were grown for 30–40 days at the following PPFD levels: ●, High = 1,500 μmol m^{-2} s^{-1}. ○, Medium = 150 μmol m^{-2} s^{-1}. △, Low = 15–25 μmol m^{-2} s^{-1}. Data are means and SE of three plants.

PPFD in *M. sobolifera* (fig. 2*B*) and highest in *M. cuspidata* in plants grown at high PPFD (fig. 4*B*).

Growth PPFD did not have a significant effect on c_i (figs. 1*C*, 2*C*, 3*C*, 4*C*). Generally, c_i was high at very low instantaneous PPFD and then decreased and remained constant at instantaneous PPFD levels above ca. 200 μmol m^{-2} s^{-1}.

Quantum yields increased with decreasing growth PPFD in *M. frondosa* and *M. sobolifera* (table 1). Quantum yield was highest at medium-growth PPFD in *M. schreberi* but highest at high PPFD in *M. cuspidata*.

A_{mes}/A ratios in *M. cuspidata* and *M. frondosa* increased with increasing growth PPFD (table 1). In *M. schreberi*, A_{mes}/A was not different between the medium and low PPFD levels, and, in *M. sobolifera*, A_{mes}/A was different only between plants from the high and medium PPFD levels.

PIGMENT RESPONSES TO PPFD

Total chl concentration increased in *M. frondosa* and *M. sobolifera* with decreasing PPFD (table 2), and a/b ratios declined at the lowest PPFD level. In both *M. schreberi* and *M. cuspidata*, chl concentration increased from high to medium PPFD and then decreased at the lowest PPFD level. Chl a/b ratios in *M. schreberi* were highest at high PPFD but remained unchanged in *M. cuspidata* at the three PPFD levels.

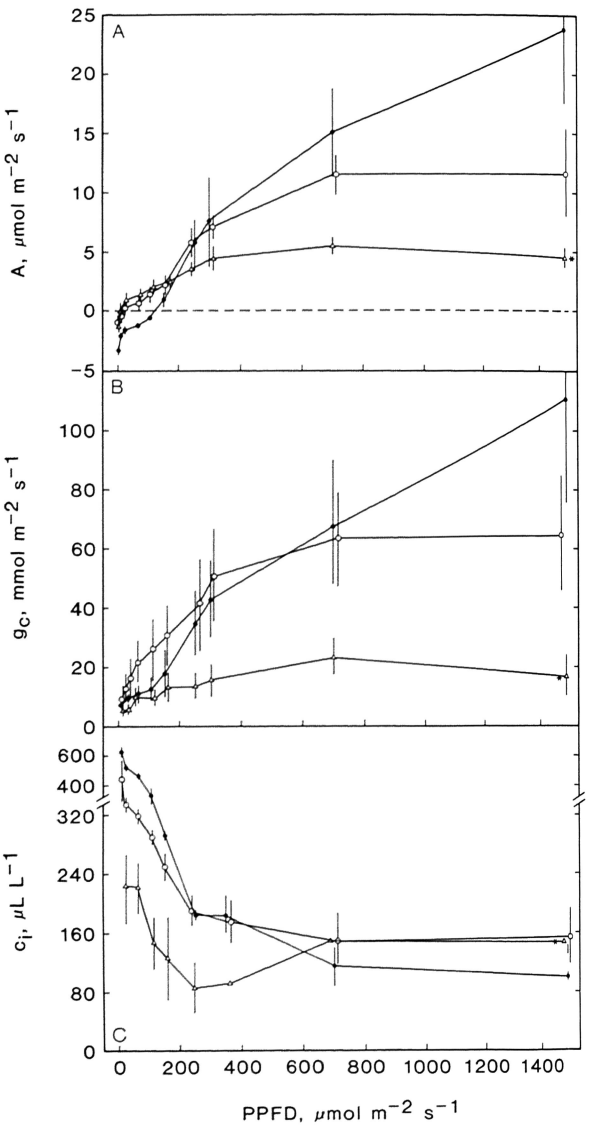

FIG. 4.—*A*, Assimilation rate (A); *B*, leaf conductance (g_c); and *C*, intercellular CO_2 concentration (c_i) as functions of PPFD in *Muhlenbergia cuspidata*. Plants were grown for 30–40 days at the following PPFD levels: ●, High = 1,500 μmol m^{-2} s^{-1}. ○, Medium = 150 μmol m^{-2} s^{-1}. △, Low = 15–25 μmol m^{-2} s^{-1}. Data are means and SE of three plants. Asterisks indicate non-steady-state results.

TABLE 1

EFFECT OF PPFD ON QUANTUM YIELD AND A_{mes}/A IN THREE UNDERSTORY AND ONE PRAIRIE SPECIES OF A C_4 GRASS AFTER 28–35 DAYS OF GROWTH IN A GROWTH CHAMBER

	Growth PPFD (μmol m^{-2} s^{-1})		
	High PPFD	Medium PPFD	Low PPFD
Species	1,500 μmol m^{-2} s^{-1} $\bar{X}$ ± SE (No.)	150 μmol m^{-2} s^{-1} $\bar{X}$ ± SE (No.)	15–25 μmol m^{-2} s^{-1} $\bar{X}$ ± SE (No.)
Muhlenbergia frondosa:			
Quantum yield	.034 (3)	.044 (3)	.053 (3)
A_{mes}/A ratio	6.71 ± .35a (5)	5.17 ± .14b (8)	4.51 ± .09c (7)
M. sobolifera:			
Quantum yield	.046 (3)	.053 (3)	.057 (3)
A_{mes}/A ratio	6.02 ± .22a (7)	5.48 ± .09b (5)	5.19 ± .17b (10)
M. schreberi:			
Quantum yield	.023 (3)	.040 (3)	.023 (3)
A_{mes}/A ratio	5.79 ± .16a (10)	5.04 ± .19a (4)	4.93 ± .16b (7)
M. cuspidata:			
Quantum yield	.028 (3)	.022 (3)	.022 (3)
A_{mes}/A ratio	20.72 ± .43a (4)	18.88 ± .31b (5)	15.63c (1)

NOTE.—Only means with different letters differ significantly ($P < .05$, Mann-Whitney U-test). Sample sizes are in parentheses after the name of each species.

PHOTOSYNTHETIC ELECTRON TRANSPORT

Rates of oxygen uptake increased with increasing growth PPFD in *M. frondosa* and *M. cuspidata* (fig. 5*A*, 5*D*) but not in *M. sobolifera* or *M. schreberi* (fig. 5B, 5C). The maximum rate of oxygen absorption was higher for *M. frondosa* grown at high and medium PPFD than in plants grown at low PPFD (fig. 5*A*), and in *M. cuspidata* the highest uptake rates occurred in plants grown at high PPFD (fig. 5*D*). In addition, maximum oxygen-uptake rates for *M. cuspidata* were twice as high as those of the other species. Although oxygen-uptake rates began to saturate at ca. 200 μmol m^{-2} s^{-1} for all species at all growth PPFD levels, plants of *M. frondosa* and *M. cuspidata* from high PPFD continued to exhibit a gradual increase in oxygen uptake up to the highest PPFD level (fig. 5*A*, 5*D*).

Discussion

PHOTOSYNTHETIC GAS EXCHANGE

The photosynthetic responses of *Muhlenbergia cuspidata* to growth PPFD are consistent with reports of a number of C_4 sun plants (BOARDMAN 1977; BJÖRKMAN 1981). Because c_i did not differ significantly among growth PPFD levels, plants of *M.*

TABLE 2

EFFECT OF PPFD ON chl CONTENT (mg g^{-1} DW) AND chl a/b RATIOS IN THREE UNDERSTORY SPECIES AND ONE PRAIRIE SPECIES OF A C_4 GRASS

	Growth PPFD (μmol m^{-2} s^{-1})		
	High PPFD	Medium PPFD	Low PPFD
Species	1,500 μmol m^{-2} s^{-1} $\bar{X}$ ± SE	150 μmol m^{-2} s^{-1} $\bar{X}$ ± SE	15–25 μmol m^{-2} s^{-1} $\bar{X}$ ± SE
Muhlenbergia frondosa (no. = 10):			
Chl content	8.80 ± 1.68a	23.02 ± 2.80b	29.68 ± 2.51c
Chl a/b ratio	3.39 ± .33a	3.34 ± .28a	3.06 ± .17b
M. sobolifera (no. = 10):			
Chl content	9.37 ± 1.40a	25.13 ± 4.06b	31.61 ± 1.68c
Chl a/b ratio	3.40 ± .24a	3.34 ± .24a	2.99 ± .23b
M. schreberi (no. = 6):			
Chl content	10.58 ± 1.30a	27.67 ± 2.7b	5.92 ± 1.42c
Chl a/b ratio	3.42 ± .10a	3.30 ± .16b	3.10 ± .57b
M. cuspidata (no. = 4):			
Chl content	14.69 ± 3.62a	19.40 ± 3.00b	10.00 ± 1.20c
Chl a/b ratio	3.80 ± .23	4.00 ± .45	4.40 ± .95

NOTE.—Only means with different letters differ significantly ($P < .05$, LSD).

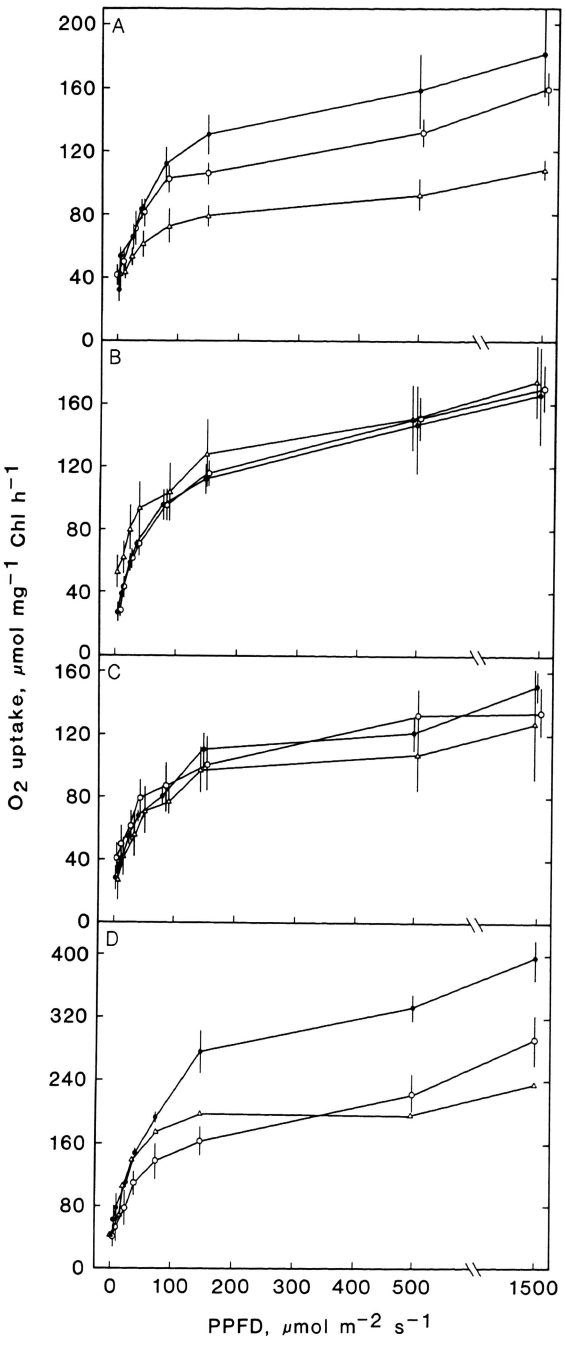

FIG. 5.—Oxygen uptake rates as a function of PPFD in photosystem I electron transport from DCIP to MV in *A*, *Muhlenbergia frondosa; B*, *M. sobolifera: C*, *M. schreberi;* and *D*, *M. cuspidata*. Plants were grown for 28–35 days at the following PPFD levels: ●, High = 1,500 μmol m^{-2} s^{-1}. ○, Medium = 150 μmol m^{-2} s^{-1}. △, Low = 15–25 μmol m^{-2} s^{-1}. Data are means and SE of three plants.

cuspidata were not metabolically damaged when grown at low PPFD, although CO_2-uptake rates were ca. 80% lower than when grown at high PPFD. Photosynthesis apparently was limited by stomatal conductance (FARQUHAR and SHARKEY 1982). On the other hand, the magnitude of the reduction in A in plants grown at low PPFD indicated that, although they appeared undamaged, they were not harvesting enough PPFD to grow well at such reduced levels. This concurred with observations that *M. cuspidata* died at the lowest PPFD before the end of the 38-day growth period (SMITH and MARTIN 1987).

The low quantum yields of *M. cuspidata* relative to other C_4 plants (EHLERINGER and BJÖRKMAN 1977; WARD and WOOLHOUSE 1986) may be the result of a glaucous, reflective leaf surface. Leaf pubescence can reduce absorption of PPFD by 20%–70% (EHLERINGER and BJÖRKMAN 1978). The lack of response to a decrease in PPFD indicates that *M. cuspidata* cannot increase its light utilization efficiency with decreasing growth light level. This is consistent with results for other high-light plants (MONSON et al. 1982; PEARCY and EHLERINGER 1984).

Muhlenbergia frondosa, M. sobolifera, and *M. schreberi* are shade adapted to some degree. None of the three suffered a reduction in maximum A between the high and medium PPFD growth regimes. While the photosynthetic rates are lower (ca. 18 μmol m^{-2} s^{-1}) than for most C_4 plants, they are comparable with those observed in other C_4 species from shaded habitats (ROBICHAUX and PEARCY 1980; WINTER et al. 1982; WARD and WOOLHOUSE 1986). Although the low PPFD plants of the understory species had lower A at 1,500 μmol m^{-2} s^{-1}, the degree of reduction was much less than that observed in *M. cuspidata*. In addition, the saturation of A with respect to PPFD in all but *M. cuspidata* is atypical of other C_4 plants, which, under optimal growth conditions, show no photosynthetic saturation at full sunlight (PEARCY et al. 1982).

Changes in quantum yield indicate a greater efficiency of light utilization at low PPFD than at high PPFD in *M. frondosa* and *M. sobolifera,* with values increasing with decreasing growth PPFD. These changes correlate with a similar increase in pigment concentrations.

The discrepancy in A between plants of *M. schreberi* from the medium PPFD regime and those from the high PPFD treatment is difficult to interpret in view of the optimal growth of this species at the highest PPFD level (SMITH and MARTIN 1987). The changes in quantum yields with PPFD in *M. schreberi,* however, are consistent with the observed responses of photosynthesis and pigments. The low quantum yield at high PPFD may be the result of photoinhibition of the photosynthetic apparatus (BJÖRKMAN 1981), whereas the low value in plants grown at low light may reflect an inability to increase pigment levels adequately (ÖQUIST et al. 1982).

Growth PPFD for *M. sobolifera* had no differential effect on either maximum A or the level of PPFD at which A saturated, indicating that this species cannot utilize increased levels of PPFD. This

agrees with the growth study in which this species exhibited equal biomass production at high and medium PPFD (SMITH and MARTIN 1987). These findings, coupled with quantum yields and chl concentrations that increased with decreasing growth PPFD, indicate that *M. sobolifera* is well adapted to the deep shade of forest understories.

RESPONSES OF A_{mes}/A TO PPFD

The values for A_{mes}/A in *M. cuspidata* are in agreement with published values for six C_4 species (LONGSTRETH et al. 1985). In the three understory species, however, A_{mes}/A is much lower because (1) chlorophyllous mesophyll tissue was extremely limited (SMITH and MARTIN 1987), and (2) bundle sheath cells, which were included in measurements made by LONGSTRETH et al. (1985), were intentionally excluded in this study since they are not exposed to atmospheric CO_2 (STAMP et al. 1985). However, meaningful comparisons of A_{mes}/A ratios can be made between the species and plants grown at different PPFD levels in our study.

In both *M. cuspidata* and *M. frondosa,* the increase in A_{mes}/A with increasing A is consistent with results for other species grown at high and low PPFD (NOBEL et al. 1975; LONGSTRETH et al. 1985). However, *M. sobolifera* and *M. schreberi* did not show a consistent positive correlation between A and A_{mes}/A. Similar results have been reported for other C_4 understory species (PEARCY et al. 1982; WARD and WOOLHOUSE 1986). Photosynthetic responses of *M. sobolifera* and *M. schreberi* evidently are limited by factors other than, or in addition to, mesophyll surface area. It is apparent that not all plants respond to changing light levels only by alteration of leaf morphology.

PIGMENT RESPONSES TO PPFD

The increase in chl concentration in response to decreasing PPFD in *M. frondosa* and *M. sobolifera* is a typical response of shade plants (BJÖRKMAN and HOLMGREN 1963; JURIK et al. 1979). In contrast, the chl concentration of sun plants either remains relatively unchanged over a range of PPFD (BJÖRKMAN 1981) or declines with severe shading (ÖQUIST et al. 1982). The response of *M. frondosa* and *M. sobolifera* clearly is atypical of sun plants. Although *M. schreberi* exhibits a similar increase in chl concentration from high to medium PPFD, its lack of response to the lowest PPFD regime indicates that it is limited in its capacity to adjust. The pigment response of *M. cuspidata* is more typical of those of sun plants. This species exhibited weaker increases in total chl in response to medium-growth PPFD and then a decline at the lowest growth PPFD level. This is an indication of the poor condition of the plants. In all growth experiments in which the other species reached maturity (ca. 38 days; SMITH and MARTIN 1987), *M. cuspidata* died at this PPFD level.

The low chl a/b ratios in *M. frondosa* and *M. sobolifera* at low-growth PPFD are consistent with their ability to tolerate shaded conditions. Low chl a/b ratios at low-growth PPFD indicate an increase in size of the light-harvesting complex (ALBERTE and THORNBER 1974). Although existing data for chl a/b ratios in sun and shade plants are not always definitive, sun plants generally do not respond with as great a reduction in a/b ratios as do shade plants (BJÖRKMAN 1981).

The increase in chl a/b ratios of *M. cuspidata* in response to decreasing PPFD during growth indicates a lack of adaptive adjustment in pigment concentrations to low levels of PPFD. In *M. schreberi* a significant decrease in chl a/b ratio occurs at medium PPFD. However, as with chl concentration, chl a/b ratios in this species do not decrease in response to the lowest growth PPFD level. This implies that it is intermediate between *M. cuspidata* from exposed habitats and both *M. frondosa* and *M. sobolifera* in its ability to adjust its pigments in response to decreasing PPFD.

PHOTOSYSTEM I ELECTRON TRANSPORT

The rates of photosystem I activity for the species in this study are comparable to those of spinach, barley, and several algae (CHUA 1971; KATOH 1972; PLESNIČAR and BENDALL 1973). The increase in electron transport through photosystem I in response to increased growth PPFD in the sun species *M. cuspidata* is consistent with results for other high-light species (BOARDMAN 1972; BJÖRKMAN 1981). Electron transport in *M. cuspidata* and *M. frondosa* responds similarly to increasing PPFD, but the maximum rates of *M. cuspidata* are twice as high as any of the other species in this study. The proportional decrease in maximum electron transport for plants of *M. frondosa* grown at the lowest PPFD level is less than that for *M. cuspidata* grown at the same PPFD level. This indicates that *M. frondosa* is more flexible in its electron-transport capacity than *M. cuspidata,* though less successful at utilizing high PPFD. These results support the photosynthetic data, in which a similar response of A to increasing growth PPFD is observed. Both *M. frondosa* and *M. cuspidata* have lower oxygen-uptake rates at the lower growth PPFD levels than *M. sobolifera* and *M. schreberi.* The latter species, though demonstrating lower electron-transport rates at the highest instantaneous PPFD level than *M. cuspidata,* have rates equally high for all growth PPFD. In *M. sobolifera,* this conforms to the pattern in the photosynthetic data.

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